

An Eocene soldierfish (Teleostei: Holocentridae) from Monte Baldo (NE Italy)

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ABSTRACT - An Eocene holocentrid fish is described herein from the southern sector of Monte Baldo, NE Italy. Although the fossil lacks the posterior portion of the body and the dense scale covering prevents the observation of the postcranial skeleton, it shows a set of morphological characters (e.g., transverse crest on the dorsal surface of supraoccipital; skull roof ornamented by ridges and channels; frontals extending posteriorly over the parietals and supraoccipital; eyes large; opercle with weakly serrated posterior margin; maxilla expanded posteriorly; two supramaxillae) that support its assignment to the family Holocentridae. Moreover, the premaxilla with an ascending process shorter than the alveolar one, the quadrate-mandibular joint located behind the posterior margin of the orbit, and the absence of a prominent preopercular spine concur to suggest a possible attribution to the subfamily Myripristinae. The family Holocentridae is represented today by squirrelfishes and soldierfishes that inhabit warm shallow waters on coral reefs and rocky bottoms up to 200 m of depth. This new specimen represents one of the few fossils of this family recovered in the Eocene deposits of the western Tethys, providing support to the hypothesis that the evolutionary origin of holocentrid fishes took place in the warm and shallow paleobiomes of this region.

INTRODUCTION

Squirrel- and soldierfishes of the family Holocentridae are small to medium sized teleostean acanthomorphs that today include about 90 species arranged in eight genera (Nelson et al., 2016; Fricke et al., 2021). They inhabit the tropical to temperate marine shallow waters of the Atlantic, Indian and Pacific Oceans, with their highest species richness in the Indo-Australian Archipelago (Dornburg et al., 2014; Nelson et al., 2016). They live on coral reefs or rocky bottoms, usually on the continental shelf, being some of the most conspicuous members of the nocturnal reef community (Randall & Greenfield, 1999; Greenfield, 2003; Nelson et al., 2016; Busserolles et al., 2021). The monophyletic status of the extant holocentrids is supported by a suite of morphological features, including a transverse crest on the supraoccipital, enlargement of the penultimate anal-fin spine, expansion of the haemal and neural spines on the fourth or fourth and fifth preural vertebrae, a hook-like process on the outermost radial of the pelvic fins, a single vertical scale row along the anterior margin of the opercle, a medial-lateral expansion of the posteriormost rib, a rostral spine in larvae and juveniles, and basipterygia with a dorsally peaked internal wing (e.g., Zehren, 1979; Stewart, 1984; Moore, 1993a). Based on the morphology of the swim bladder and auditory bulla, Nelson (1955) classified the holocentrids in two subfamilies: Myripristinae (soldierfishes) and Holocentrinae (squirrelfishes). Subsequent studies find support to the dichotomous nature of the Holocentridae based, e.g., on the presence or absence of a long preopercular spine, position of the quadrate-mandibular articulation with respect to the orbit,

and the relative development of the ascending and alveolar processes of the premaxilla (Zehren, 1979; Stewart, 1984).

Despite the monophyly of the family and the two subfamilies has been demonstrated based on both morphology and molecules (see Dornburg et al., 2012), there is still a general disagreement about the phylogenetic relationships of the Holocentridae within the Acanthomorpha. Holocentrids have been traditionally included within the order Beryciformes and considered to be closely related to the Anomalopidae, Anoplogastridae, Berycidae, Diretmidae, Monocentridae, and Trachichthyidae (e.g., Johnson & Patterson, 1993; Colgan et al., 2000; Miya et al., 2003; Nelson, 2006; Wiley & Johnson, 2010; Near et al., 2012). However, several morphological and molecular studies recovered the Beryciformes sensu Johnson & Patterson (1993) to be paraphyletic, and the Holocentridae as sister to the Percomorpha (e.g., Stiassny & Moore, 1992; Moore, 1993b; Betancur-R et al., 2013, 2017; Davesne et al., 2016; Hughes et al., 2018). For this reason, Betancur-R et al. (2013) proposed a new monotypic order, the Holocentriformes, to include the sole family Holocentridae.

Although several putative fossil holocentrids were reported from Upper Cretaceous deposits (e.g., †*Alloberyx*, †*Caproberyx*, †*Paracentrus*, †*Pelotius* and †*Trachichthyoides*), these are currently regarded as stem holocentrids (or holocentroids) because Cenozoic and extant holocentrids are united by synapomorphies not shared by these Cretaceous taxa (Stewart, 1984; Patterson, 1993). With the possible exception of †*Pelotius* from the Turonian of Brazil (Gallo-Da-Silva & De Figueiredo, 1999), crown holocentrid genera based on complete

or partially complete articulated skeletal remains are only known from Cenozoic deposits, and include †*Berybolcensis*, †*Eoholocentrum* and †*Tenuicentrum* from the lower Eocene of Monte Bolca (Sorbini, 1975, 1984; Sorbini & Tirapelle, 1975), †*Holocentrites* from the Eocene-Oligocene of Florida (Conrad, 1941; Dunkle & Olsen, 1959), and †*Africentrum* from the Miocene of the Mediterranean region (e.g., Woodward, 1887; Bassani, 1911; D'Erasmus, 1924; Arambourg, 1927; White & Moy-Thomas, 1941), together with some fossil species assigned to extant genera (e.g., Bannikov, 1987) and species (Sorbini, 1988). However, some authors disagree about the placement of some of these Cenozoic taxa within the Holocentridae, as †*Africentrum* is sometimes placed in Trachichthyidae (e.g., Kotlarczyk et al., 2006), and †*Berybolcensis* and †*Tenuicentrum* are regarded as stem holocentrids by Dornburg et al. (2014). Other fossil genera considered to be putative holocentrid fishes, including †*Naupygus* and †*Paraberyx* from the lower Eocene London Clay Formation (Casier, 1966), †*Holocentroides* from Oligo-Miocene of Eastern Europe (Paučá, 1931), †*Plagiolocentrum* from the Oligocene of Austria (Rabeder, 1978) and †*Pseudholocentrum* from the Eocene of Iran (Arambourg, 1967) are only known based on fragmentary material or have not been thoroughly described, and therefore their attribution to the Holocentridae is regarded as ambiguous (see, e.g., Bannikov, 1987). A few genera and species of fossil holocentrids were also described based on otoliths (e.g., Frizzel & Lamber, 1961; Stinton, 1978; Schwarzahns, 1980, 1984; Schwarzahns & Bratishko, 2011).

In this paper, we describe a single fish specimen coming from middle Eocene beds of the Paleogene succession of the southern sector of Monte Baldo, near the locality of Cambrigar (Verona Province; NE Italy). Despite its incompleteness, the fossil exhibits a set of anatomical features that support its recognition as a myripristine holocentrid fish.

GEOLOGICAL AND PALEONTOLOGICAL SETTING

Geology

The fossil comes from an outcrop near Cambrigar, a hamlet of the town of Ferrara di Monte Baldo, which is located in the southern sector of the Monte Baldo mountain chain, between the Garda Lake and the Adige River, about 40 km from the city of Verona (NE Italy; Fig. 1). During the Paleogene, the area was part of the western margin of the “Lessini Shelf”, a carbonate platform superimposed on the Late Jurassic to Paleocene Trento Plateau (Bosellini, 1989). Such a structural domain of the Adria Plate, characterised by pelagic/hemipelagic sedimentation, reacted rigidly during the Alpine collision and was segmented into

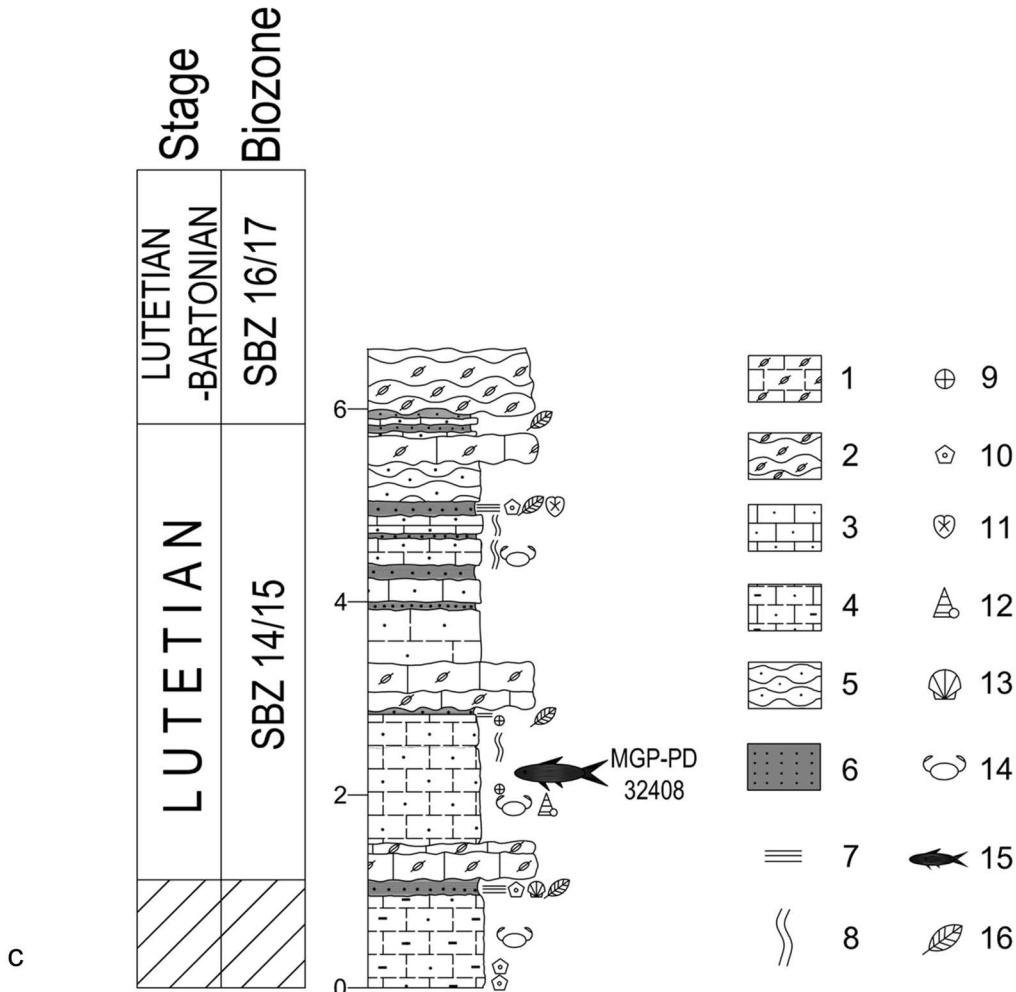
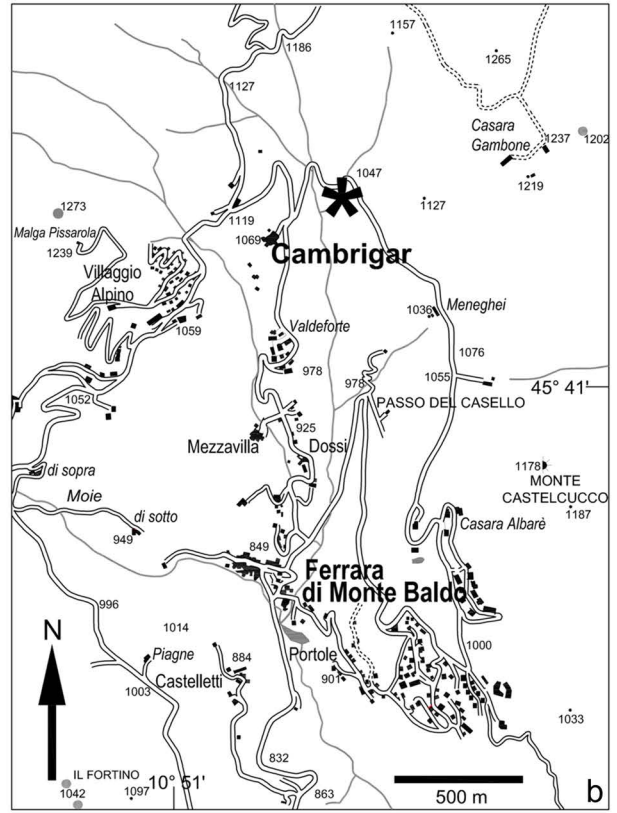
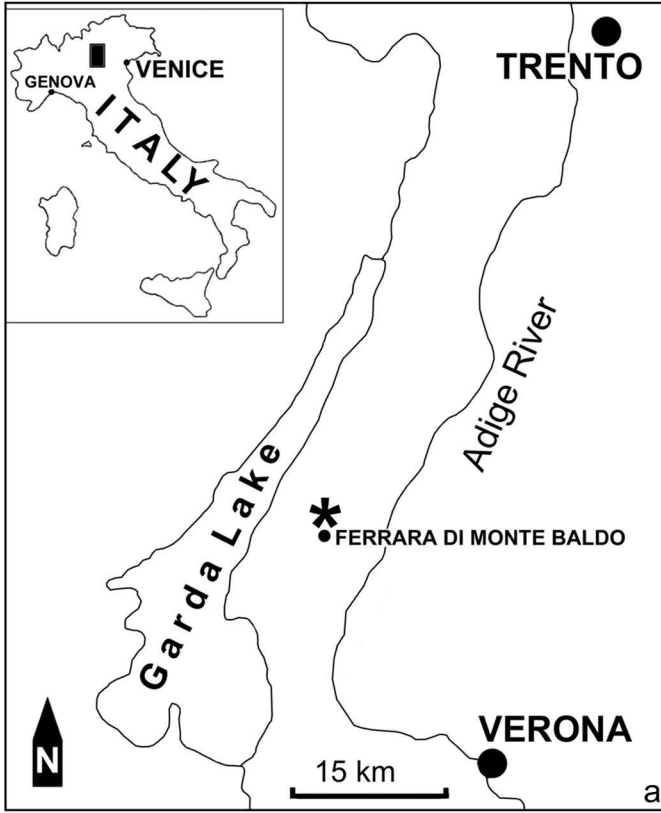
variously uplifted blocks that acted, since the early Eocene, as centres of initiation of shallow water carbonates, which finally coalesced resulting in the formation of the Lessini Shelf (Doglioni & Bosellini, 1987; Bosellini, 1989; Luciani, 1989).

The Paleogene sedimentary succession of Monte Baldo lies unconformably on the Upper Cretaceous (Turonian-Maastrichtian) hemipelagites of the Scaglia Rossa Formation and has been framed by Luciani (1989) into four depositional sequences: Torbole sequence (early-middle Eocene p.p.), Nago sequence (middle Eocene p.p.-late Eocene p.p.), Acquenere sequence (late Eocene p.p.-early Oligocene) and Monte Brione sequence (late Oligocene). In the surroundings of Cambrigar (southern sector of Monte Baldo), the Torbole depositional sequence is represented by the “Calcicare di Chiusole” and “Calcicare di Malcesine” formations, overlaid by the “Calcicare di Nago” and “Marne di Bolognano” formations of the Nago sequence. The lower Eocene “Calcicare di Chiusole” is generally composed of well-bedded micritic limestones with planktonic foraminifera and/or carbonate turbidites of neritic origin deposited in a bathyal context. This unit grades upward into the coarser lower-middle Eocene limestones of “Calcicare di Malcesine”, which testifies to slope deposits, capped by the middle-upper Eocene “Calcicare di Nago”, consisting of coarse calcirudites, sometimes silicified or glauconitised, rich in larger foraminifera and deposited in shallow waters. Bioherms with corals irregularly associated with biocalcirudites occur in the upper portion of this unit. The Paleogene stratigraphic succession in the Cambrigar area ends with the upper Eocene-lower Oligocene “Marne di Bolognano” formation that marks the establishment of a relatively deep depositional environment (Luciani, 1989).

Paleontological context

The sedimentary succession of the Torbole depositional sequence cropping out in the surroundings of Ferrara di Monte Baldo is renowned for its fossil crabs, probably known since the first decades of the nineteenth century (Beschin & De Angeli, 2011). The first documented mention of these findings, however, seems to be that of the geologist Enrico Nicolis (1882, p. 81) who reported the occurrence of *Cancer punctulatus* Desmarest, 1822 associated with “algae and *Pentacrinus* sp.” within the marls cropping out at “Ardeforte a monte di Ferrara” (presently Valdeforte; Fig. 1). The brachyurans from this locality were subsequently discussed by Bittner (1884) and De Gregorio (1895). Ramiro Fabiani (1915), in his monumental monograph on the Paleogene of Veneto region, described the fossiliferous content of lower Eocene “marls” cropping out between Mezzavilla and “Ardeforte”, not far from Cambrigar, reporting the presence of the crinoid “*Pentacrinus*” *diaboli* Bayan, 1870 and the crab *Harpactocarcinus punctulatus* (Desmarest, 1822) along with not better specified plant and fish remains (Fabiani,

Fig. 1 - Geographic position of Cambrigar (indicated with the asterisk), Ferrara di Monte Baldo, Verona Province (a, b), and (c) stratigraphic log and larger benthic foraminiferal biozonation (SBZ) of the fossiliferous site (lower Cambrigar section; below) according to Serra Kiel et al. (1998). 1, calcirudites with larger foraminifera, locally glauconitic; 2, subnodular calcirudites with larger foraminifera, locally glauconitic; 3, calcarenites, locally glauconitic; 4, marly calcarenites, locally glauconitic; 5, subnodular calcarenites; 6, calcarenitic marls; 7, laminations; 8, bioturbations; 9, Fe-sulfides nodules; 10, columnals of crinoids; 11, irregular echinoids; 12, gastropods; 13, pectinids; 14, crabs; 15, MGP-PD 32408; 16, vegetal remains.



1915). More recently, Luciani (1989) briefly mentioned the presence of 20 meters of fine-grained calcarenites at Cambrigar with “*Pentacrinus*” *diaboli* showing a facies lithologically transitional from the “Calcare di Chiusole” to the “Calcare di Malcesine”. Later on, some papers renewed the interest in the fossil carcinofauna of the area describing two new taxa (an anomurid and a brachyuran; Garassino et al., 2009; Beschin & De Angeli, 2011; Beschin et al., 2016) and recognising the presence of *Harpactocarcinus macrodactylus* (Milne Edwards in D’Archiac, 1850) among the brachyurans previously referred to *H. punctulatus* (see Beschin & De Angeli, 2011). Despite their evident paleontological relevance, the fossiliferous beds of Ferrara di Monte Baldo are still in need of detailed stratigraphical and paleontological investigations.

The lower Cambrigar section

The fossil fish described herein was discovered in 2011 by a private collector, Mr. Luigi Ambrosi, in a section cropping out along the right bank of a stream incision about 500 meters NE of Cambrigar, referred to as “lower Cambrigar section” (Fig. 1). The outcrop consists of a package of six meters of greyish marly calcarenites and light brown calcarenites with subordinate greyish and brownish marls intercalated by three larger foraminifera-bearing calciruditic beds (Fig. 1). The measured section is capped by a thick pile of subnodular and irregularly bedded larger foraminifera-bearing calcirudites and calcarenites of which only the basal 75 cm were logged (Fig. 1). Based on its lithological features, the outcrop can be referred to the Calcare di Malcesine Formation or, alternatively, to the transition from the Calcare di Chiusole to the Calcare di Malcesine Formation. The depositional paleoenvironment, as previously mentioned, is most probably in slope deposits, with redeposition of shallow-water biota transported downslope. The articulated fish skeletal remain described herein represents the only fossil vertebrate recovered to date in the site and come from a 1.5 m-thick package of calcarenites, locally glauconitic with Fe sulphide nodules and bioturbations filled by larger foraminifera (Fig. 1). More than ten years of researches in the site yielded also scattered specimens of brachyurans recovered in each calcarenitic interval of the section (Figs 1 and 2a-b). The most common fossils occurring in the outcrop, however, are represented by columnals of *Isselocrinus diaboli* (Bayan, 1870), quite abundant in the basal greyish marly calcarenites, small pectinids (*Propeamussium* sp.; Fig. 2c), gastropod internal moulds and irregular echinoids (Fig. 1). Vegetal remains preserved as impressions covered by orange to brown limonite powder also occur (Fig. 2e-f), especially in the marly beds (Fig. 1), and are mostly represented by macroalgae, likely referable to *Delessertes* (Fig. 2e). The rocky debris in close vicinity to the outcrop also yielded a large fossil fruit (Fig. 2d), an angiosperm leaf (Fig. 2f) and seagrasses preserved within fine-grained calcarenites, whose precise stratigraphic position is unknown.

Biostratigraphic assignment of the section and age of the fossil fish

The age of the lower Cambrigar section was estimated based on larger foraminifera coming from the four calciruditic intervals represented in the logged section (Fig. 1). The determination relies on random thin sections; therefore, the specific attributions could retain some degree of uncertainty. Even with this premise, the larger foraminiferal assemblages are quite consistent throughout the section and allow to distinguish two intervals, the lower one containing *Nummulites alponensis* Schaub, 1981 and the upper one with *N. biarrizensis* d’Archiac & Haime, 1853, *N. discorbinus* (Schlotheim, 1820), and *N. millicaput* Boubée, 1832. Therefore, according to Schaub (1981) and Serra-Kiel et al. (1998), it is possible to refer most of the section to the SB14-15 combined Zones, whereas the upper portion can be assigned to the SB16-17 combined Zones (Fig. 1). In terms of standard stages this means middle Lutetian (SB14-15) and upper Lutetian-lower Bartonian (SB16-17).

The fish specimen that was collected from the calcarenitic interval bounded by the first and second calciruditic bed (Fig. 1) is therefore ascribed to the middle Lutetian, around 45-42 Ma (see Speijer et al., 2020).

MATERIAL AND METHODS

This study is based on a single specimen still partially embedded in the sedimentary matrix and housed in the Museo di Geologia e Paleontologia dell’Università degli Studi di Padova, Italy, under catalogue number MGP-PD 32408. The specimen was studied using a Leica M80 stereomicroscope equipped with camera lucida drawing arms. Before examination, the specimen required matrix removal that was achieved using entomological needles in order to allow investigation of its anatomical details. Osteological terminology mainly follows Zehren (1979) and Stewart (1984). Comparative morphological data were derived from the literature (e.g., Conrad, 1941; White & Moy-Thomas, 1941; Sorbini, 1975, 1984; Sorbini & Tirapelle, 1975; Zehren, 1979; Stewart, 1984; Gallo-Da-Silva & De Figueiredo, 1999).

SYSTEMATIC PALEONTOLOGY

Order HOLOCENTRIFORMES Betancur-R et al., 2013
Family HOLOCENTRIDAE Richardson, 1846
Subfamily MYRIPRISTINAE Nelson, 1955

Genus and species indet.
(Figs 3-6)

Material - MGP-PD 32408; a fish specimen lacking the posterior part of the body (Fig. 3).

Fig. 2 - (color online) Selected fossils recovered from the lower Cambrigar section. a) The crab *Harpactocarcinus macrodactylus* (Milne-Edwards in d’Archiac, 1850), dorsal view, scale bar: 20 mm. b) *Harpactocarcinus macrodactylus* (Milne-Edwards in d’Archiac, 1850), ventral view of the specimen in (a), scale bar: 20 mm. c) The pectinid *Propeamussium* sp., scale bar: 5 mm. d) Strongly compressed fossil fruit possibly belonging to *Nypa* (MGP-PD 32409), scale bar: 50 mm. e) Slab with several small leaf-like thalli of the marine macroalga *Delessertes*, scale bar: 50 mm. f) Leaf of an undetermined angiosperm, scale bar: 20 mm.

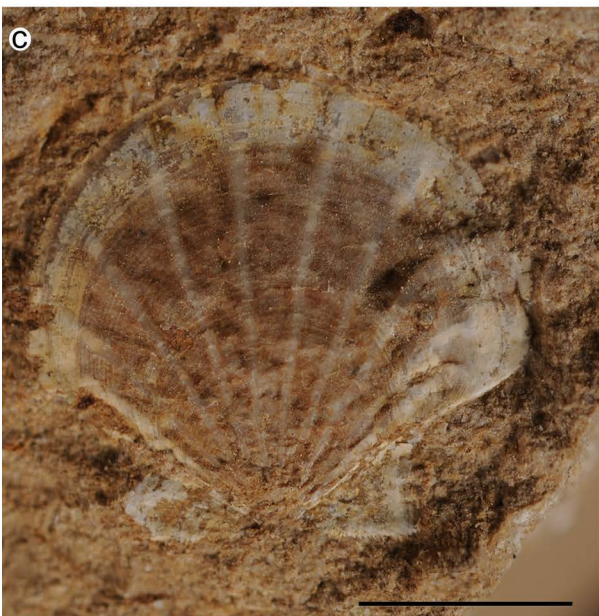
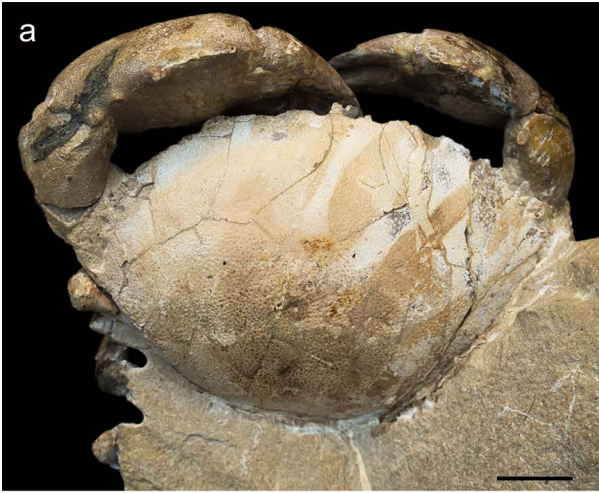




Fig. 3 - (color online) Myripristinae, gen. et sp. indet., MGP-PD 32408, from the Lutetian of Monte Baldo, Italy. Left lateral view. Scale bar: 30 mm.

Occurrence - Cambrigar, Ferrara di Monte Baldo (Verona Province; northeastern Italy); middle Lutetian, ca. 45-42 Ma.

Measurements (in millimeters) - Head length = 69.0; head depth = 72.4; preorbital length = 4.1; postorbital length = 36.9; orbit diameter = 25.0; sclerotic ring diameter = 14.8; maximum body depth = 102.2; predorsal distance = 129.6.

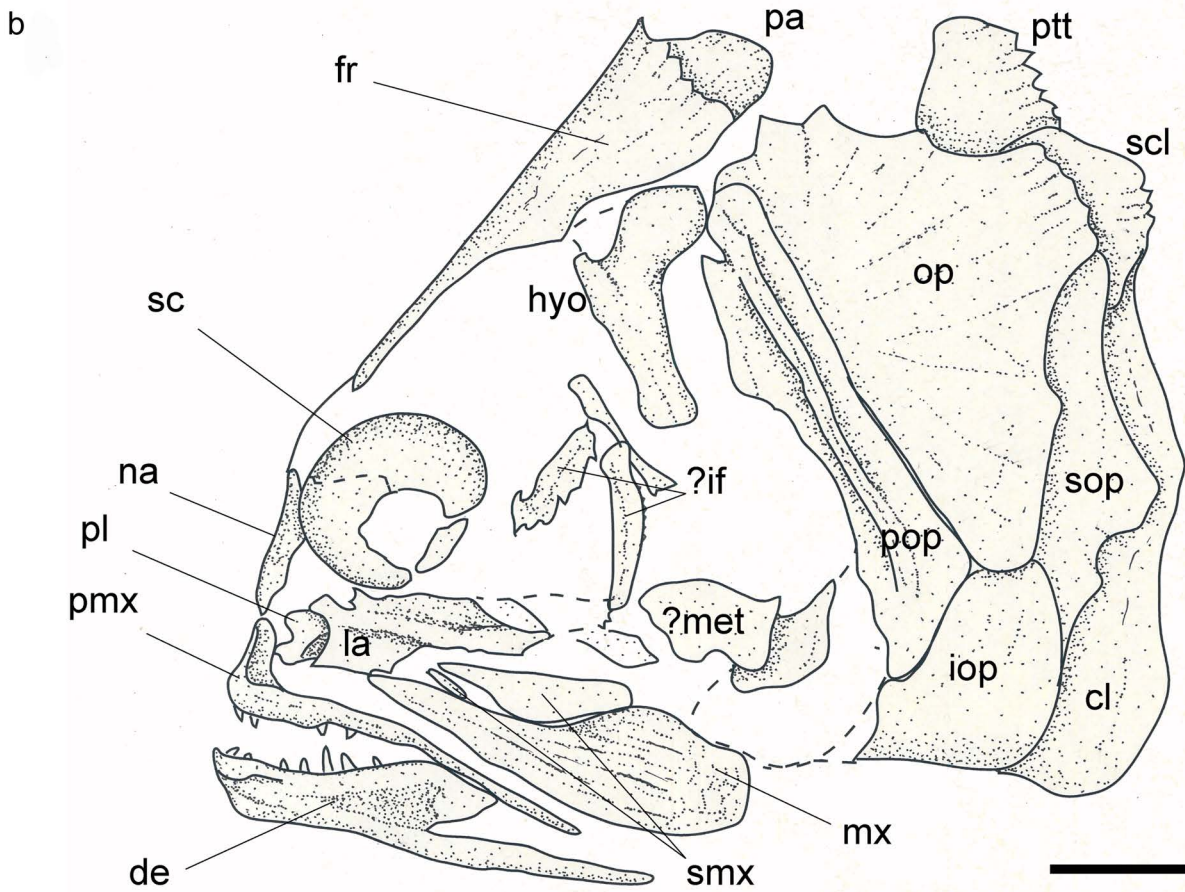
Description - The fossil consists of an incomplete and three-dimensionally preserved articulated fish lacking the posterior part of the body and still partially embedded in the calcareous matrix (Fig. 3). The left side of the fossil is exposed showing the entire head as well as the anteriormost part of the trunk, including some dorsal-fin spines. The body is moderately large, laterally compressed and characterised by a large orbit and a small mouth. The structure of the postcranial skeleton cannot be determined, being enclosed in the scale cover and the sedimentary matrix.

The head is deep, slightly higher than long, and with a steep and obtuse frontal-nasal profile (Fig. 4). The skull

roof (Fig. 5) is almost completely occupied by the frontals, which are antero-posteriorly elongated, subtrapezoidal in shape and extend posteriorly over the parietals and part of the supraoccipital. As the frontals extend almost to the posterior margin of the skull roof, the supratemporal fossa is difficult to detect. The frontals are ornamented with ridges and channels that run antero-posteriorly, possibly representing the mucous cavities typical of holocentrids (e.g., Patterson, 1964). The parietals are in large part covered by the frontals (Fig. 5). The supraoccipital extends forward separating the frontals in their posterior portion (Fig. 5). A transverse crest marks the posterior edge of the supraoccipital ending in a long and thin medial spiny process that projects caudally (= spina occipitalis of Allis, 1909). The parasphenoid is barely visible just below the orbit and appears as a long and thin bone. The other bones of the neurocranium are not visible. The nasals appear as paired, subrectangular bones located just anterior to frontals and possibly in contact with each other along their entire medial margin.

The infraorbitals are quite shallow and surround the ventral and posterior margin of the orbit (Fig. 4). The first infraorbital (lachrymal) is the largest of the series

Fig. 4 - (color online) a) Myripristinae, gen. et sp. indet., MGP-PD 32408, from the Lutetian of Monte Baldo, Italy. b) Reconstruction of the head and pectoral girdle. Abbreviations: cl, cleithrum; de, dentary; fr, frontal; hyo, hyomandibula; if, infraorbitals; iop, interopercle; la, lachrymal; met, metapterygoid; mx, maxilla; na, nasal; op, opercle; pa, parietal; pl, palatine; pmx, premaxilla; pop, preopercle; ptt, posttemporal; sc, sclerotic ring; scl, supraclathrum; smx, supramaxillae; sop, subopercle. Scale bars: 20 mm.



and possesses a spiny ventral margin; it is spatulate anteriorly and tapers posteriorly, bearing an anteromedial facet that probably articulated with the lateral ethmoid in origin. It is difficult to detect the original morphology of the second and third infraorbitals, whereas the other infraorbitals appear taphonomically displaced from their original position. The ratio between the largest depth of the first two infraorbitals compared to their combined length is about 1:4, like in myripristines (in holocentrines the ratio ranges from 1:4.4 to 1:7; Stewart, 1984). The large space delimited by the infraorbitals, frontals and nasals suggests the presence of very large eyes in origin. There is an ossified and robust sclerotic ring, possibly formed by two elements.

The premaxilla is well developed and bears small ascending and articular processes, as well as a very long alveolar process (Fig. 4), similar to those of several extinct Cretaceous holocentroids and modern myripristines (Stewart, 1984). The oral border of the premaxilla bears a single row of small conical teeth. The premaxilla excludes almost completely the maxilla from the oral gape. The maxilla is antero-posteriorly elongate, with a straight, elongate, and almost cylindrical anterior shaft and a large and spatulate posterior edge. The posterior half of the maxilla is ornamented with thin and antero-posteriorly directed ridges, like in several fossil and recent holocentrids (e.g., Zehren, 1979; Stewart, 1984). The oral margin of maxilla is edentulous. There are two supramaxillae lying on the dorsal border of the maxilla. The anterior one is small, thin, and rod-like, whereas the posterior supramaxilla is large and paddle shaped. Both the supramaxillae do not appear ornamented, contrary to the condition observed in the Eocene †*Berybolcensis* and †*Eoholocentrum* from Bolca (Sorbini & Tirapelle, 1975; Sorbini, 1984). The dentary is robust, moderately deep, bearing a short coronoid process and a long and narrow ventral process. Its alveolar platform is expanded near the symphyseal area and overhangs the lateral side of the dentary as in †*Eoholocentrum*, †*Berybolcensis*, †*Holocentrites* and extant myripristines (Stewart 1984). It is difficult to detect the mandibular sensory canal on its ventral margin. The anguloarticular is poorly preserved and it is hard to properly determine its articulation with the quadrate, although it is likely that the quadrate head was placed behind the posterior margin of the orbit, like in extant myripristines (Zehren, 1979; Stewart, 1984).

The suspensorium is poorly preserved (Fig. 4), solely represented by part of the hyomandibula and fragments of the palatine and of what appears to be a metapterygoid, although we cannot exclude that this latter might represent part of the horizontal arm of the preopercle. Although the hyomandibula is incomplete, it appears narrow and elongate, with a slightly expanded articular head. There is not the enlarged foramen for the hyomandibular trunk of the seventh cranial nerve, which characterises the extinct genus †*Holocentrites* (Stewart, 1984). It is difficult to detect whether the dorsal portion of the hyomandibula bears one or two articular heads for the neurocranium. The palatine is largely incomplete solely represented by its anteriormost portion.

Of the preopercle, only its vertical arm and the posteroventral angle are preserved (Fig. 4). The vertical branch is long and narrow and has a smooth posterior

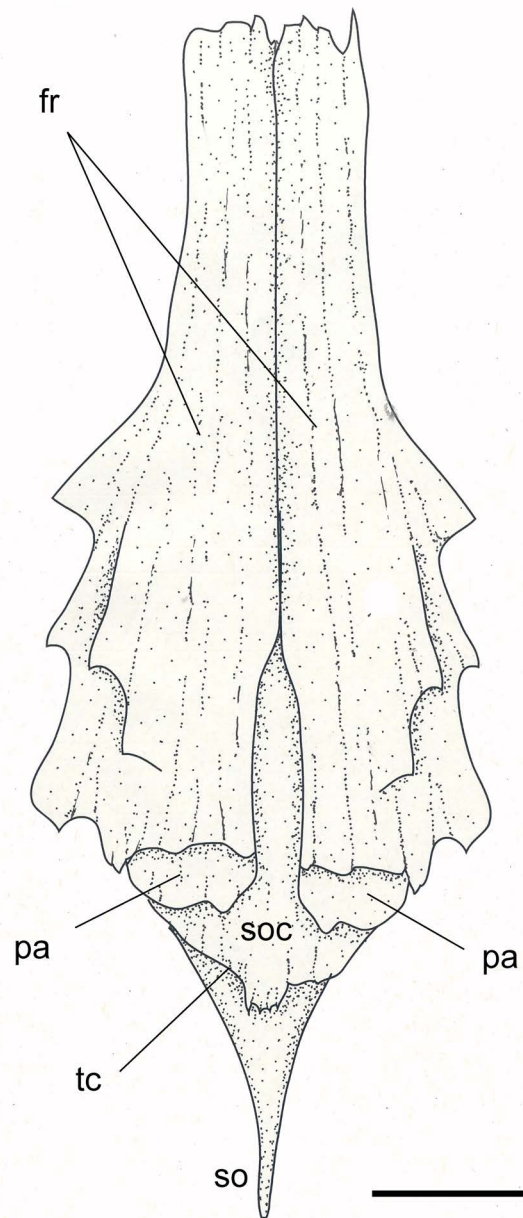


Fig. 5 - Myripristinae, gen. et sp. indet.; MGP-PD 32408 from the Lutetian of Monte Baldo, Italy. Reconstruction of the skull roof. Anterior upward. Abbreviations: fr, frontals; pa, parietals; so, spina occipitalis; soc, supraoccipital; tc, transverse crest. Scale bar: 10 mm.

margin. The posteroventral angle of the preopercle lacks the long spine that typically characterises the holocentrines (Zehren, 1979; Stewart, 1984). The opercle is large, about twice as deep as broad and quadrangular in shape, with a straight anterior margin and a weakly serrated posterodorsal border; there are a few striations that extend from the anterodorsal margin to the posterior edge, and no scales on the anterior border of the opercle, showing a condition similar to that of the Cretaceous holocentrid †*Pelotius*. The subopercle is small, while the interopercle is incomplete, with only its posterior part being visible ventral to the other bones of the opercular series. The hyoid apparatus is not preserved.

The posttemporal is well ossified and shows serrations along its posterior border; its dorsal and ventral branches



Fig. 6 - (color online) Myrpristinae, gen. et sp. indet.; MGP-PD 32408 from the Lutetian of Monte Baldo, Italy. Scales from the thoracic region. Anterior to the left. Scale bar 20 mm.

are not preserved. The supracleithrum is small and also shows a serrated posterior border. The cleithrum is crescent-shaped, apparently devoid of serrations along its posterior margin. Coracoid, scapula and most of the pectoral fin are not preserved (Fig. 4b). A few pectoral-fin rays lie just posterior to the cleithrum. The preserved portion of the dorsal fin is only represented by the first three or four dorsal-fin spines. The soft portion of the dorsal fin is not preserved.

The trunk is entirely covered by large crenate scales (sensu Roberts, 1993) showing simple ridges and indentations along their posterior margin but no true spines (Fig. 6). This condition is not known in extant holocentrids, which usually exhibit spinoid scales (i.e., posterior margin with spines which are continuous with the main body of the scale), whereas extinct genera like †*Pelotius* and †*Tenuicentrum* are characterised by cycloid scales. However, crenate scales have been reported for the Upper Cretaceous holocentroid †*Paracentrus* (Forey et al., 2003). Nevertheless, it is not possible to conclusively exclude that weak and small spines were present along the posterior margin of the scales in origin, which were lost due to taphonomic processes. The squamation of the specimen consists of at least ten horizontal scale rows. Due to inadequate preservation it is not possible to detect the lateral-line scales.

DISCUSSION

The osteological analysis clearly supports the assignment of the examined specimen to the Acanthomorpha based on presence of true spines in the dorsal fin and the spina occipitalis on the supraoccipital bone (Johnson & Patterson, 1993; Wiley & Johnson, 2010).

Despite several studies that contributed to the understanding of the anatomy of extinct holocentrid fishes (e.g., Conrad, 1941; Dunkle & Olsen, 1959; Patterson, 1964, 1967; Sorbini, 1975, 1984; Sorbini & Tirapelle,

1975) their relationships with the crown members of the family Holocentridae were difficult to determine until the 1980s. This was mostly due to the discovery of several Upper Cretaceous holocentrid-like taxa (e.g., †*Alloberyx*, †*Caproberyx*, †*Paracentrus*, †*Trachichthyoides*) whose peculiar combination of characters made it necessary to emend the definition of the family (Patterson, 1967; Gallo-Da-Silva & De Figueiredo, 1999).

Zehren (1979) listed five characters that support the monophyly of the family Holocentridae, including a transverse crest on the supraoccipital; posterior process of the basiptyrgium expanded into a plate; hook-shaped process on the most external pelvic radial; enlarged penultimate anal-fin spine; distal expansion of the neural and haemal spines of the fourth or fourth and fifth preural vertebrae. Subsequently, Gayet (1980) added the presence of a complete vertical row of scales along the anterior edge of the opercle; disappearance of the sixth hypural; single caudal complex formed by the first preural centrum and the first and second ural centra; dorsal fin with two lobes; “beryciform” foramen (fenestra to the hyoideal efferent artery) on the ceratohyal reduced or absent; and two supraneurals. Gayet (1982) created the superfamily Holocentroidea to include the families Pycnosteroididae, Stichocentridae and Holocentridae, based on the shared possession of three synapomorphies, including a subocular shelf along all the infraorbitals; frontals posteriorly developed covering the supratemporal fossa; and parietal and pterotic separated. This hypothesis, however, was reconsidered and the families Stichocentridae and Pycnosteroididae were regarded as Acanthomorpha incertae sedis or, at least, the Pycnosteroididae as either member of the Lampridomorpha (Davesne et al., 2014; Delbarre et al., 2016), or sister to a clade that includes *Polymixia*, †*Omosomopsis*, †*Sphenocephalus*, and Percopsiformes as successive sister taxa to a clade that unites Gadiformes, Zeiformes, and *Stylephorus* (Davesne et al., 2016).

In defining the Holocentridae, Stewart (1984) added the medial-lateral expansion of the last pleural rib. Stewart (1984) also produced a morphology-based phylogenetic analysis including putative fossil and extant holocentrids. According to this analysis, also supported by Patterson (1993), unambiguous fossils of the Holocentridae appeared in the Cenozoic, and include the extinct genera †*Africentrum*, †*Berybolcensis*, †*Eoholocentrum*, †*Holocentrites* and †*Tenuicentrum*, while all the Cretaceous genera (e.g., †*Alloberyx*, †*Caproberyx*, †*Paracentrus*, †*Trachichthyoides*) must be considered as stem holocentrids, which are united to the Cenozoic genera by a single character, the expansion of the neural spine of the fourth or of the fourth and fifth preural centrum, respectively (Stewart, 1984; Forey et al., 2003).

Moore (1993a) provided two additional synapomorphies that support the monophyly of the family Holocentridae, a rostral spine in larvae and juveniles formed by modified nasal bones supported by an enlarged ethmoidal cartilage, and basiptyrgia with a dorsally peaked internal wing, giving the pair of bones a unique shape of an elongate tetragonal disphenoid.

Dornburg et al. (2014), adapting the character list from Stewart (1984) and Moore (1993a, b), provided the most recent attempt to produce a morphology-based

calibrated phylogenetic tree useful for biogeographic reconstructions. In their analysis, the early Eocene †*Berybolcensis* and †*Tenuicentrum* are considered stem holocentrids supporting the hypothesis of a western Tethyan origin for the family. The Eocene-Oligocene †*Holocentrites* is recovered as stem Myripristinae, whereas the Miocene †*Africentrum* is sister to *Myripristis*. Finally, the early Eocene †*Eoholocentrum* is resolved as sister to the subfamily Holocentrinae (Dornburg et al., 2014). Dornburg et al. (2014) did not include †*Pelotius* in their analysis but regarded it as a holocentroid fish.

Despite its incompleteness and partially inadequate preservation, the specimen MGP-PD 32408 can be unquestionably assigned to the Holocentridae based on the presence of a transverse crest on the dorsal surface of supraoccipital. Moreover, the fossil exhibits a combination of morphological features identified by Patterson (1964) and Nelson et al. (2016) as diagnostic of holocentrids, including a moderately deep and compressed trunk, eyes large, opercle with spiny posterior edge, skull roof ornamented by ridges and channels, frontals extending posteriorly over the parietals and supraoccipital, infraorbitals with subocular shelf, maxilla expanded posteriorly, and two supramaxillae, of which the posterior one characterised by a process overlapping the anterior.

Both Zehren (1979) and Stewart (1984) concur to suggest that the two monophyletic holocentrid subfamilies, Holocentrinae and Myripristinae, can be distinguished from each other based on a suite of morphological characters. For example, holocentrines are characterised by the presence of a large and pointed spine at the posterior angle of the preopercle, which is greatly reduced or absent in myripristines; the quadrate-mandibular articulation lies anteriorly to the posterior border of the orbit in holocentrines, whereas it is positioned in the rear of the orbit in myripristines; the ascending ramus of the premaxilla is equal to or longer than the alveolar arm in holocentrines, and shorter in myripristines. Based on these features, Stewart (1984) assigned all the extinct Cenozoic genera †*Africentrum*, †*Berybolcensis*, †*Eoholocentrum*, †*Holocentrites*, and †*Tenuicentrum* to the Myripristinae.

Although the incompleteness of the body and postcranial skeleton makes this attribution only tentative, it is reasonable to hypothesise that the specimen MGP-PD 32408 pertains to the Myripristinae based on the absence of preopercular spine, ascending process of premaxilla shorter than the alveolar one, and quadrate-mandibular joint lying in the rear of the orbit. This specimen differs from the other fossil myripristine genera by having a unique combination of morphological features. The absence of scales on the opercle allows distinguishing it from the other fossil holocentrids (except †*Pelotius*), which show a partial (†*Eoholocentrum*, †*Holocentrites*, †*Africentrum*) or an almost complete cover (†*Berybolcensis*, †*Tenuicentrum*) of opercular scales (see Conrad, 1941; White & Moy-Thomas, 1941; Sorbini, 1975, 1984; Sorbini & Tirapelle, 1975). The presence of crenate scales distinguishes it from †*Pelotius* and †*Tenuicentrum* that are characterised by cycloid scales (Sorbini, 1975; Gallo-Da-Silva & De Figueiredo, 1999). Finally, the specimen MGP-PD 32408 can be distinguished from †*Holocentrites* because of the absence of the enlarged foramen for the hyomandibular trunk of the seventh cranial nerve (Stewart, 1984).

The assignment of MGP-PD 32408 to any of the extant myripristine genera can be ruled out based on the absence of some of the diagnostic characters listed by Stewart (1984). Its alignment with *Myripristis* can be ruled out because of the anterior extension of the supraoccipital that separates the frontals posteriorly (vs. frontals in contact with each other along their entire midline) and the absence (vs. presence) of maxillary teeth. MGP-PD 32408 differs from *Ostichthys* by having nasals subparallel along their median edges (vs. greatly diverging anteriorly). Finally, the fossil described herein does not show the posteriorly directed hypertrophied spines on the infraorbitals and preopercle that characterise *Corniger*, or the second supraoccipital transverse crest forming a second angular ridge that is characteristic of *Plectrypops* and *Holotrachys*. However, until additional better-preserved and more complete material would be available, it is not possible to properly define the relationships of the fossil documented herein, nor conclusively demonstrating its separate generic placement.

Squidrelfishes and soldierfishes today inhabit tropical to warm temperate coastal biotopes, being commonly associated to coral reefs and rocky bottoms rarely up to 200 m. They are mostly nocturnal fishes, usually hiding in crevices or beneath ledges of reefs in the daytime (Randall & Greenfield, 1999; Greenfield, 2003; Nelson et al., 2016; Busserolles et al., 2021). From this perspective, the presence of a holocentrid fish in the Lutetian of Cambrigar, might suggest that it was transported downslope from its life environment, most probably from a warm and shallow paleobiotope, possibly characterised by reefs and/or rocky bottoms.

The western Tethys marks the earliest record of many extant tropical fish lineages, including the teleost families Acanthuridae, Antennariidae, Apogonidae, Ephippidae, Labridae, Pomacentridae, Siganidae (e.g., Bellwood, 1996; Bellwood & Wainwright, 2002; Carnevale & Pietsch, 2009; Bannikov & Carnevale, 2010) and the batoids Neotrygoninae, Hypolophinae and Urogyminae (Marramà et al., 2018, 2019; Adnet et al., 2019). In this perspective, the fossil described herein represents an additional occurrence of the Holocentridae in the Eocene deposits of the western Tethys, along with those from the Ypresian of Bolca and the Priabonian of Brendola (Sorbini, 1975, 1984; Sorbini & Tirapelle, 1975; Gayet & Barbin, 1994), providing support to the hypothesis that the evolutionary origin of the holocentrid fishes took place in the warm and shallow waters of the western Tethys (Dornburg et al., 2014).

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